Impoverishment of Soil Fauna Due to Agriculture

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Animals exert two general types of functional influences on agroecosystems. The first type comprises activities that either directly or indirectly result in a noticeable influence on yield (e.g., feeding on agricultural crops, dissemination of pathogens, pollination of plants, etc.). The second type concerns a direct or indirect influence of a much lower intensity, the effects of which are cumulative and may be noticeable only after a longer period of time (e.g., influences on humification and mineralization of organic matter and on matter cycling, interactions with soil microorganisms, impacts on soil structure and its physicochemical conditions, etc.). Phenomena of the first type are well known, but studies concerning the second type and the essential role of animals in maintaining soil fertility have been initiated only recently.

IMPOVERISHMENT OF SOIL FAUNA IN AGROECOSYSTEMS

The functional significance of animals in an ecosystem depends primarily on their density and biomass; however, little is known about the overall biomass of animals living in soils of various ecosystems. The first reliable estimates of total edaphon density and biomass were published after the International Biological Programme was initiated, but only a few studies incorporated Protozoa.

The only full estimates of the biomass of all animals living in the soil of cultivated fields have been obtained in studies conducted in the Department of Agrobiology and Forestry, Polish Academy of Sciences, in Poznań (Ryszkowski 1979, 1981). The estimated edaphon biomass, including Protozoa, ranged from approximately 1.9 g dry wt/m^2 in a wheat field to almost 4.5 g dry wt/m^2 in a rye field (Table 1). Differences were due to large variations in protozoan biomass, which is conditioned by soil moisture, the concentration of soil bacteria, and root exudates. In soil under rye cultivation, the estimated biomass of Protozoa was 5.7 g dry wt/m^2 in one analysis, whereas a month later, the estimated biomass in the same field was only 0.2 g dry wt/m^2. Similarly, studies on meadow soil have shown significant changes in protozoan biomass, ranging from 0.04 to 0.54 g dry wt/m^2.

Studies conducted by R. Paprocki (personal communication) have indicated that protozoan biomass in cultivated fields is similar to or even exceeds that of

meadow soil. In both soils, amoebae were predominant and constituted 44 to 86% of the overall protozoan biomass.

Protozoa feeding on bacteria accelerate nutrient turnover and appear to promote the biochemical activity of the soil. Thus, a higher biomass of Protozoa in an agroecosystem could indicate a more rapid turnover of nutrients as well as a higher decomposition rate of organic matter.

Without Protozoa, the edaphon biomass in an agroecosystem averaged approximately 1.5 g dry wt/m^2 (Table 1). The exclusion of Protozoa enables a comparison of the edaphon biomasses in agroecosystems with estimates obtained for other types of terrestrial ecosystems, such as those of Ghilarov and Chernov (1975) (Table 2). By a compilation of data, they estimated that biomasses of soil fauna in various non-agarian ecosystems in the temperate zone of the USSR range from 5.4 to 45 g dry wt/m^2. About 2,000 years ago, deciduous forests covered the cropland area of Turew, where data for Table 1 were gathered (Z. Wojcik, personal communication). Assuming that Ghilarov and Chernov's data for soil fauna biomass in deciduous forests approximate the edaphon biomass in Turew soils before cultivation, it is possible to estimate that the Turew soil fauna diminished from 18-45 g dry wt/m^2 to 1.5 g dry wt/m^2 over a period of 2,000 years due to tillage.

In recent years, two direct estimates have been published concerning the overall

Table 1. Mean standing crop estimates (g dry wt/m^2) of soil fauna in cropland at Turew, Poland.

Taxon	Potato field[a]	Rye field[a]	Wheat field[a]	Meadow[b]	Source of data[c]
Winged insects (mainly larvae)	0.089	0.1094	0.0622	4.8830	Nabiałczyk-Karg 1980, J. Karg
Lumbricidae	0.770	0.840	0.940	3.8400	Jopkiewicz 1972, Ryl 1984
Nematoda	0.201	0.3190	0.5574	0.8166	Wasilewska 1974, 1979, Wasilewska and Paplińska 1975, T. Witkowski
Acarina	0.0049	0.0077	0.0112	0.3050	Wasylik 1975, D. Sell
Enchytraeidae	0.1913	0.1312	0.0509	0.1986	Ryl 1977, 1980, B. Ryl
Collembola	0.0511	0.0813	0.0474	0.0656	Czarnecki 1979, A. Czarnecki
Subtotal	1.3073	1.4886	1.6691	10.1088	
Protozoa	3.0000[d]	3.0000[d]	0.2010[e]	0.2400[e]	[d]Rough estimate by J. Eismond-Karabin, [e]R. Paprocki
Total	4.3073	4.4886	1.8701	10.3468	

[a]Cultivated soils are pseudo-podzolic with 0.6% organic carbon (see Margowski et al. 1976 for more detail).

[b]Meadow soil is muck with 7.0% organic carbon (Z. Prusinkiewicz).

[c]Personal communication where year is not given.

Table 2. Biomass estimates (g dry wt/m^2) of soil fauna in terrestrial ecosystems of the temperate climatic zone (without Protozoa).

Type of estimate	Deciduous forest	Deciduous-coniferous forest	Coniferous forest	Grassland	Agroecosystem
Approximate	18.0-45.0[a]	9.0-12.0[a]	5.4-9.0[a]	6.0-9.0[a]	
Direct	3.5[b]			32.200[d]	1.700[m]
	20.562[c]			10.291[e]	1.669[n]
				10.108[f]	1.488[o]
				4.370[g]	1.307[p]
				2.567[h]	
				1.863[i]	
				1.629[j]	
				0.852[k]	
				0.823[l]	

[a] Various uncultivated ecosystems, temperate zone of USSR (Ghilarov and Chernov 1975; converted to dry weight by Ryszkowski, assuming a mean water content of soil animals of 70%).
[b] Oak-ash, England (Satchell 1971).
[c] *Liriodendron tulipifera*, USA (Reichle 1977).
[d] Meadow steppe, USSR (French et al. 1979).
[e] Pasture, Australia (Hutchinson and King 1979).
[f] Meadow, Poland (Ryszkowski, see Table 1 this paper).
[g] Mixed prairie, Canada (Coupland and Van Dyne 1979).
[h] Central mixed prairie, USA (Dyer 1979).
[i] True prairie, USA (Dyer 1979).
[j] Maintained grassland, USA (Dyer 1979).
[k] Northern short-grass prairie, USA (Dyer 1979).
[l] Southern short-grass prairie, USA (Dyer 1979).
[m] Wheat field, USSR (French et al. 1979).
[n] Wheat field, Poland (Ryszkowski, see Table 1 this paper).
[o] Rye field, Poland (Ryszkowski 1979 modified).
[p] Potato field, Poland (Ryszkowski 1979 modified).

edaphon biomass without Protozoa (Table 2). Both estimates were higher for deciduous forest soils than for cultivated soils, although in an oak-ash forest in England (Satchell 1971) the difference was only 2.5-fold. Among nine estimates obtained for prairie grassland ecosystems, four characterized by low rainfall had biomass levels similar or even lower than those in the soils of cultivated fields.

Three cultivated fields near Turew, Poland, had edaphon biomasses (without Protozoa) more than 6-fold less than in an adjacent meadow (see Table 1). A simi-

lar difference has been observed between the edaphon of a pasture and that of cultivated fields (Hutchinson and King 1979, Table 2). The biomass of a meadow steppe edaphon was almost 20 times higher than that in a nearby cultivated wheat field (French et al. 1979, Table 2). All the above data indicate that unless limited by lack of moisture, edaphon biomass is lower in cultivated fields than in forests and grassland ecosystems.

The biomasses of winged insect larvae and Lumbricidae differed between the cultivated fields and the meadow near Turew (Table 1). Insect larvae biomass was 78-fold greater in the meadow soil than in the wheat field soil. Diptera constituted 74.2% of all winged insect larvae in the meadow soil, and only 29.9% in the wheat field soil, where Coleoptera were dominant with a biomass of 0.034 g dry wt/m^2 (J. Karg, personal communication) and included the very mobile Carabidae and Cantharidae. The biomass of Lepidoptera larvae was 0.0087 g dry wt/m^2 in the wheat field soil and slightly higher in the meadow, amounting to 0.0132 g dry wt/m^2.

The biomass of Lumbricidae in the meadow soil was four times larger than in soil under wheat cultivation (Table 1). The meadow had seven species of earthworms, the wheat field only three (Ryl 1984). Predominant both in the meadow and cultivated field was *Allolobophora caliginosa*. There were more juveniles in the cultivated fields than in the meadow, which indicates a higher turnover rate of earthworm communities in cultivated fields.

The meadow also contained a higher biomass of nematodes than the soils of the three cultivated fields (Table 1). These findings conform with the results of a recently conducted analysis of nematode occurrence in basic terrestrial ecosystems (Wasilewska 1979). In this analysis, the highest nematode biomass levels were determined in grassland ecosystems, intermediate levels in agroecosystems, and lowest levels in forests. A low biomass of nematodes in forest ecosystems results from fewer nematode herbivores when compared with grasslands and agroecosystems. The fact that gramineous plants stimulate the growth of nematode biomass was confirmed by greater concentrations of nematodes in rye and wheat field soils than in soil under potato cultivation (Table 1). Although nematode biomass is lower in agroecosystems than in grasslands, the amount of organic matter they decompose during respiration is higher in agroecosystmes than in grasslands (Wasilewska 1979) and evokes a higher turnover rate of nutrients.

Compared with the meadow, a dramatic decrease in Acarina was observed in the cultivated fields (Table 1), due primarily to the lack of a litter layer. Among the few mites occurring in the agroecosystems, predatory forms were prevalent. However, the biomass of mites in the meadow was not large when compared with that of winged insects, earthworms, and nematodes; thus, Acarina was of secondary importance in the general diminution of soil fauna in the agroecosystems.

Our long term studies on cultivated fields have shown that ants, snails, millipedes, and centipedes are practically eradicated from agroecosystems.

Similar to Protozoa, no decrease in Enchytraeidae and Collembola biomass was observed in cultivated fields when compared with meadow conditions (Table 1). Using Enchytraeidae biomass estimates from various agroecosystems near

Turew and data from the literature, Ryl (1980) concluded that the biomass of these animals in cultivated fields is similar to the mean biomass levels determined for other terrestrial ecosystems. In fertile meadows and forests, Enchytraeidae biomass may be two or three times higher than in cultivated fields. These analyses indicate that Enchytraeidae are well adapted to changing conditions in cultivated fields. Ryl stressed that not only cosmopolitan species and those commonly occurring in various soils of Europe, but also species considered more typical for natural habitats, are found in cultivated fields. Their small body sizes and the ability to regenerate injured parts may account for the success of this animal group in agroecosystems.

Collembola biomass levels determined in the cultivated fields and meadow near Turew (Table 1) are similar to or slightly lower than those reported for five grassland ecosystems in Europe (Healey 1971).

Soil fauna constituted over 90% of all animals occurring in the agroecosystems studied at the Department of Agrobiology and Forestry, including not only aboveground invertebrates, but also all vertebrates (Ryszkowski 1979, 1981). It can thus be assumed that the process of fauna diminution due to agriculture concerns all animals, not only those of the edaphon.

CHANGES IN TROPHIC STRUCTURE OF SOIL FAUNA IN AGROECOSYSTEMS

The division of animals into three basic trophic groups—herbivores, saprophytes, and carnivores—is still important even at the present, unsatisfactory state of our knowledge about edaphon feeding habits. Despite various inaccuracies, this classification enables us to estimate what percentage of the fauna participates in energy flow and matter cycling based on the grazer food web (herbivores), and what percentage leads a scavenger's life (saprophytes). The carnivore category deliminates secondary, tertiary, and even higher trophic level consumers in the ecosystem.

During 1979, saprophytes were clearly dominant in the soils of both the wheat field and the neighbouring meadow at Turew, although the level of saprophagous forms in the wheat field was lower than in the meadow (Table 3). The percentage of herbivores was higher in the soil of the wheat field, whereas the level of carnivores was similar in both ecosystems. The trophic structure of the whole edaphon was determined by the abundance of saprophagous earthworms and the trophic differentiation of larvae of winged insects and nematodes.

The percentage of herbivores among wheat field winged insects amounted to 36%, while their contribution was only 23% in the meadow (Table 3). The higher level of saprophytes in the winged larvae community of the meadow is connected with a greater abundance of organic matter and lack of tillage in meadow soil.

In the meadow, the herbivorous Elateridae were prevalent, constituting 93% of all herbivorous winged insects determined (J. Karg, personal communication). Species characterized by long developmental cycles, from several months to several years, dominated in this group. Tillage prevents the development of most Elateridae species and is one of the main reasons for the 142-fold biomass decrease

Table 3. Trophic structure (mg dry wt/m²) of soil fauna in a wheat field and a meadow (1979).

Taxon	Wheat field			Meadow			Trophic category determined by:[a]
	Herbivore	Saprophyte	Carnivore	Herbivore	Saprophyte	Carnivore	
Pterygota (mainly larvae)	22.40	19.20	20.60	1124.40	3637.70	120.90	J. Karg
Lumbricidae	0.00	940.00	0.00	0.00	3840.00	0.00	B. Ryl
Nematoda	390.00	167.40	0.00	562.70	252.90	0.98	T. Witkowski
Acarina	0.23	3.98	7.03	2.38	274.50	28.12	D. Sell
Enchytraeidae	0.00	50.90	0.00	0.00	198.60	0.00	B. Ryl
Collembola	0.10	47.30	0.00	5.30	57.00	3.30	A. Czarnecki
Total	412.73	1228.78	27.63	1694.78	8260.70	152.50	
Contribution to total biomass (%)	24.7	73.6	1.7	16.7	81.8	1.5	

[a]Personal communications.

exhibited by these insects in the wheat field soil when compared with the meadow soil (0.0074 g dry wt/m^2 versus 1.056 g dry wt/m^2, respectively). In the wheat field soil, Elateridae larvae constituted 33% of all winged insect herbivores, and Lepidoptera herbivores made up 39%. Chrysomelidae and Curculionidae larvae migrate from plants into the soil in order to pupate and do not ingest nutrients in the soil. Consequently, these larvae do not influence the nutrient reserves in the soil, although they may be fed on by various predators.

The mean standing crop of Diptera in the meadow soil was 3.625 g dry wt/m^2, while in the wheat field it was 0.0186 g dry wt/m^2 (J. Karg, personal communication). Among saprophytic larvae of Diptera in the meadow soil, Bibionidae and Tipulidae were the most numerous. Kozlovskaya and Zaguralskaya (1967) determined high levels of ammonification bacteria in the alimentary tracts of these two groups, indicating the occurrence of larvae of these insects may be important for the mineralization of organic nitrogen. Among herbivorous Diptera, especially in the wheat field soil, there were numerous Cecidomyidae (J. Karg, personal communication), which according to Kozlovskaya and Zaguralskaya (1967) have enzymes in their alimentary tracts capable of breaking down cellulose. If this observation is correct, this is the only group among Diptera capable of decomposing cellulose. The occurrence of Cecidomyidae larvae may thus accelerate the decomposition of wheat cellulose, which is normally decomposed slowly by bacteria.

Because there are no predatory nematodes in the soils of cultivated fields (Wasilewska 1974, 1979), the low biomass of nematodes in the meadow suggests that it had been transformed by humans, as was confirmed by Wasilewska (1979). The investigated meadow is in fact intensively fertilized and mowed twice a year. In the seven grassland ecosystems analyzed by Wasilewska (1979), the biomass of predatory nematodes averaged 11% of all nematodes, whereas in the analyzed meadow the biomass of predatory nematodes was only 0.12%. The percentage of herbivorous nematodes was 69% in the analyzed meadow, almost identical to the 70% of herbivorous nematodes in the wheat field soil.

For the remaining, less numerous systematic groups of the edaphon (Table 3), predatory Acarina constituted 63% of all mites occurring in the wheat field soil. These are mobile forms, often moving on the soil surface.

BODY WEIGHTS AND RESPIRATION RATES OF EDAPHON IN THE CULTIVATED FIELD AND MEADOW

Smaller body sizes were detected in many groups of edaphon when the body weight distribution of animals living in the cultivated fields were compared with those populating the meadow (Table 4). Differences in mean body sizes were especially distinct in the winged insect larvae, with those in the meadow soil being about 7.4-fold heavier than mean body weights of larvae found in the wheat field soil. Elateridae from the meadow soil attained an estimated average body weight of 21.6 mg dry wt, while those from the wheat field soil amounted to 9.2 mg dry wt. This trend was also very clear in Diptera. The mean body weight of these larvae in

Table 4. Body weight distribution of edaphon and energetic cost of metabolism at 15°C.

	Winged insect larvae		Lumbricidae		Nematoda		Acarina		Enchytraeidae		Collembola		Total edaphon	
	Wheat field	Meadow	Wheat field	Meadow	Wheat field	Meadow	Wheat field	Meadow	Wheat field	Meadow	Wheat field	Meadow	Wheat field	Meadow
Individual weight (mg live wt)	5.75	42.75	506.0	317.0	0.000637	0.000788	0.0104	0.0107	0.161	0.192	0.0052	0.0055		
Metabolism rate ($\mu l\ O_2/h \cdot mg$ live wt)	0.257	0.177	0.111	0.121	1.414	1.360	0.839	0.831	0.502	0.486	0.952	0.945		
Taxon respiration ($\mu l\ O_2/h \cdot m^2$)	40.0	2160.7	524.2	2337.2	2628.2	3703.2	23.5	634.2	196.7	742.8	112.8	155.0	3525.4	9733.1
Standing crop (mg dry wt/m^2)	62.2	4883.0	940.0	3840.0	557.4	816.6	11.2	305.0	50.9	198.6	47.4	65.6	1669.1	10108.8

the meadow was 19 mg dry wt, while in the wheat field it was 1.1 mg dry wt (J. Karg, personal communication). Smaller differences were found in nematodes and enchytraeids. Acarina and Collembola showed the smallest differences in body sizes, but slightly larger animals were still characteristic for the meadow.

Diminution of standing crops corresponded with decrease of mean body weights in all groups of edaphon, except Lumbricidae, Lepidoptera, Chrysomelidae, and Cantharidae. Smaller earthworms were living in the soil of the meadow than in the soil of the wheat field, although a higher percentage of juvenile forms was found in the soils of the cultivated fields. For example, the average weight of adult individuals of *Allolobophora caliginosa* was 0.61 g live wt in the wheat field and 0.53 g live wt in the meadow, and in *Lumbricus terrestris*, 2.71 g live wt and 2.5 g live wt, respectively (Ryl 1984).

Among Lepidoptera larvae in the cultivated field soil, large plant pests like *Agrotis* sp. predominated, feeding on plant roots. Chrysomelidae take advantage of soil only to pupate. Cantharidae are large mobile predators, wandering over many cultivated fields.

The well-known inverse relationship between body weight and respiration describes the mineralization efficiency of various sizes of animals. Reichle (1971) estimated the parameters of the allometric equation relating body weight and respiration, using 107 values from the phyla Nematoda, Annelida, Mollusca, and Arthropoda. Using 199 values and the same four phyla, I (Ryszkowski 1975) found almost the same parameters. My estimate was

$$y = 0.357x^{0.813}$$

where $y = \mu l\ O_2\ /h \cdot$ animal and x = mg live wt. This equation was used to calculate the respiration rate (at 15°C) for the mean body weights of individuals in distinguished taxons of the edaphon. Nematodes found in the wheat field soil showed almost 13-fold higher respiration rates per mg live weight than earthworms found in the same field (Table 4). Because of their bigger size, the earthworms in the cultivated field soils maintain their biomass at a lower energy cost than do the earthworms in the meadow. If the respiration rates per body unit of Lumbricidae living in the wheat field soil were the same as earthworms in the meadow soil, the mineralization rate of organic matter would be about 10% higher than it was approximated in reality.

Both in the wheat field and in the meadow, nematodes showed the highest respiration per square meter (Table 4). Lumbricidae and winged insects had high and almost equal contributions to the total edaphon respiration of the meadow ecosystem, whereas respiration of winged insects in the wheat field soil exceeded only Acarina.

The overall respiration rate of the meadow edaphon was approximated as 9733 $\mu l\ O_2\ /h \cdot m^2$ at 15°C. In the wheat field soil, the edaphon respiration was 3525 $\mu l \cdot O_2\ /h \cdot m^2$, or 35% of edaphon respiration in the meadow. The biomass of edaphon in the wheat field was 16% of the biomass in the meadow. Thus, eliminating bigger soil animals by tillage results in increased mineralization of organic mat-

ter per unit of biomass, because smaller surviving animals have higher metabolic rates.

FUNCTIONAL CHANGES OF EDAPHON DUE TO AGRICULTURE

Balance of organic matter providing regeneration of humus is essential for long-term management practices in agroecosystems. Fertilization, many forms of tillage, etc., increase decomposition processes, while crop removal, wind, and water erosion decrease storage of humus in soils of agroecosystems. Animals play important roles in controlling the rate of decomposition, especially due to their interactions with microbes. Complicated and very little known relationships between the input of organic matter, heterotroph (microbe and animal) respiration, and humification are the reasons why balance of organic matter in soil is achieved today by trial and error.

The findings of this study indicate that the impoverishment of soil fauna in cultivated fields corresponds to an overall increase of herbivores in the standing crop of the total edaphon, is correlated with an overall diminution of mean body weights, and is accompanied by an increased respiration rate per biomass unit. Thus, despite a 6-fold diminution of soil fauna in the studied agroecosystem in comparison to the meadow, only a 2.7-fold decrease in respiration per unit area was found. These results show that edaphon could play an important role in controlling the decomposition rate of organic matter, especially in the balance of organic matter inputs and outputs.

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